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**MODELING THERMOREGULATION IN *PEROMYSCUS***

By

Jake Gutkes

B.S. University of Maine 2018

A THESIS

Submitted in Partial Fulfillment of the

Requirements of the Degree of

Master of Science

(in Zoology)

School of Biology and Ecology

The University of Maine

August 2019

Advisory Committee:

Danielle Levesque, Assistant Professor of Mammalogy and Mammalian Health, Advisor

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# **MODELING THERMOREGULATION IN *PEROMYSCUS***

By Jake Gutkes

Thesis Advisor: Dr. Danielle Levesque

An Abstract of the Thesis Presented

In Partial Fulfillment of the Requirements for the

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Thermoregulation of animals is becoming an increasingly important field as climate change begins to affect ambient temperature and precipitation. Understanding animals' thermoregulatory properties allows us to monitor potentially vulnerable species. For my thesis, I examined the thermoregulation of *Peromyscus* and *Mus musculus* using flow-through respirometry and thermal imaging. The original goal was to create a working model for thermoregulation in *Peromyscus leucopus* and *maniculatus* but, due to lack of specimens, I examined lab mice as a comparison. Some information was already known from earlier studies and the present study aimed to update physiological information on mice. I hypothesized that higher temperatures would lead to increases metabolic rate and water loss and that the tail would be a major contributor to the radiative heat loss. Mice were placed in respirometry chambers at temperatures of 25, 30, and 35°C. At 25°C, the animals displayed the highest metabolic rate and evaporative water loss likely due to an increased level of activity. Due to high activity at the beginning of the experiment, data from 25°C were omitted from the analyses. The highest evaporative water loss for both lab and field mice was at 35°C. Field mice also had the highest metabolic rate at 35°C. However, lab mice displayed an almost equivalent metabolic rate at 30°C and 35°C. The tail did

not dissipate as much heat as the back of the mouse, indicating that the tail may only play a secondary role in thermoregulation or heat dissipation at higher temperatures.

## **ACKNOWLEDGEMENTS**

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## CHAPTER 1: INTRODUCTION

### Climate Change

Animals around the world are facing major problems caused by climate change (Pecl et al. 2017). Some species, like the white footed mouse (*Peromyscus leucopus*), are expanding poleward towards more temperate climates (Roy-Dufresne et al. 2013). Not all species are able to shift their range due to physical barriers, like mountains, or ecological boundaries, like food sources or predation (Janzen 1967; Pigot and Tobias 2013; Ghalambor et al. 2014). In the case where an animal cannot move to a more suitable climate, they must adopt other strategies to escape the higher temperatures such as: using microclimates (Tattersall et al. 2012); using behavioral or nocturnal shifts, such as reducing activity during the hotter portions of the day; or diurnal animals becoming more crepuscular, as well as changing torpor or hibernation patterns (Boutin and Lane 2014). Increased average global temperature means that many animals will be facing new abiotic stressors, which can result in a variety of negative effects.

Over the course of the last century, scientists have begun to document the changes that animals and plants are making in response to new climates (Roy-Dufresne et al. 2013; Boutin and Lane 2014; Pecl et al. 2017). Phenological shifts can be a problem; with warming temperatures, plants are flowering sooner and out of cycle with when hibernators emerge in the spring. If the hibernators do not shift with their primary food source, in this case flowering plants, they will be missing a valuable feeding time in their life (Boutin and Lane 2014). With increased variability in temperature, some hibernators also experience more periods of rewarming, which are the most costly portion of hibernation (Thomas et al. 1990). The cost of rewarming is evident in wood frog (*Lithobates sylvaticus*) populations, which have begun to decline due the increased energy demand from more thaw/freeze cycles throughout the year

(Sinclair et al. 2013). Breeding seasons are also beginning to shift earlier in the year (Boutin and Lane 2014). The increased variability of seasons may even make it difficult for species to adapt to the changing climates (Nadeau et al. 2017). This variability may cause successive bottlenecks by going from a cold year directly into an excessively hot year. Some predictions of climate change estimate a potential for 1/6 of the species to go extinct due to climate change (Urban 2015). Further predictions state that, even if we can stay under the 2°C change permitted by the Paris Agreement, there will still be major heat waves that can cause human casualties in some megacities (Matthews et al. 2017).

### **Thermoregulation**

Thermoregulation is the process by which organisms regulate internal body temperature to maintain homeostasis. Animals can roughly be separated into two major groups, endotherms or ectotherms. Ectothermic animals do not produce heat internally to help regulate internal body temperature. To thermoregulate, ectotherms use predominantly behavioral strategies to regulate body temperature. These behavioral strategies are basking, moving, increasing or decreasing surface area, and using microclimates (Crawshaw 2003; Tattersall et al. 2012; McCafferty et al. 2017). Endotherms are animals that can regulate body temperature physiologically, with either shivering or non-shivering thermogenesis (Pigot and Tobias 2013). Endotherms regulate their body temperature using the hypothalamus, the ‘thermometer’ of the body (Satinoff and Rutstein 1970; Wright et al. 2015).

An animal can exchange heat with its environment in three different ways: conduction, convection, and radiation (McCafferty 2007). Conduction, heat transfer through direct contact, is the most efficient method of heat transfer because it involves the greatest number of molecules in contact between which heat can be transferred. Convective heat loss happens over a wider area

of the body – any portion of the body that is not in contact with another object – than conductive heat loss. Radiation is the heat experienced from sunlight or its reflection off of any surface (McCafferty 2007). Solar radiation can have large effects on the operative temperature of an animal, especially desert species. The rock hyrax (*Procavia capensis*) stays under rocks or in the shade during the hot portions of the day because, at ambient temperatures of 22-25°C and in direct sunlight, they began to show signs of hyperthermia (Bartholomew and Rainy 1971). Similar behavior is observed in kangaroos; during the hottest parts of the day, kangaroos will dig to get to cooler soil and stay in shade (Dawson et al. 2000). The shade and digging decreases solar radiation and increases conductive cooling, respectively. Convective heat loss predominates in high winds, which move more air around the body and result in more heat being transferred to the surroundings (Cross et al. 2016). Thus, wind is a crucial factor in the ‘real feel’ or operative temperature, which is the temperature that is directly experienced by an organism (Sears et al. 2016).

Endotherms can employ several tactics to regulate body temperature: behavioral changes, postural changes, using microclimates, moving, basking, vasomotion, evaporative water loss, shivering, and non-shivering thermogenesis (Tattersall et al. 2012). Some eutherian mammals create heat is through uncoupling protein 1 (UCP1) (Gaudry and Campbell 2017). UCP1 acts to uncouple heat from ATP production during the electron transport chain at the end of cellular respiration. UCP1 is initiated by norepinephrine, but the majority of thermoregulatory functions are controlled by hypothalamus (Seebacher 2017). Thermogenesis is common in the brown adipose tissue (BAT). The BAT have more mitochondria than a regular adipose cell, allowing for more heat production than the average cell (Seebacher 2017). Brown adipose tissue is not found in all endotherms (Gaudry and Campbell 2017). Behavioral changes, postural changes,

microclimates, and basking are all similar in the fact that they reduce exposure to poor ambient conditions. Behavioral changes, such as nesting or huddling, can reduce exposed surface area (Gordon 2012; Boratyński et al. 2015). Postural changes affect how much of the body is exposed by changing physical shape: a sphere has a small amount of exposed surface area compared to a cylinder (McNab and Morrison 1963). Microclimates and basking involve the animal moving to more favorable conditions, thus changing the temperature the animal experiences. The more favorable environments, those closer to the thermoneutral zone (TNZ), can be underground, in the shade, in direct sunlight, or any other place that changes the temperature experienced by the animal. The TNZ is the range of temperatures where an animal spends the least amount of energy to regulate body temperatures (Figure 1.1). Animals' metabolic rates are commonly tested while rested or in small enclosures to gather resting metabolic rate (Morrison and Ryser 1959). In warm temperatures, activity can increase cooling demands on an animal (Humphries and Careau 2011). However, at colder temperatures or any temperature below the TNZ of an endotherm, activity can substitute for thermogenesis. This activity substitution can account for as much as 37% of metabolic costs of heat production (Humphries and Careau 2011).

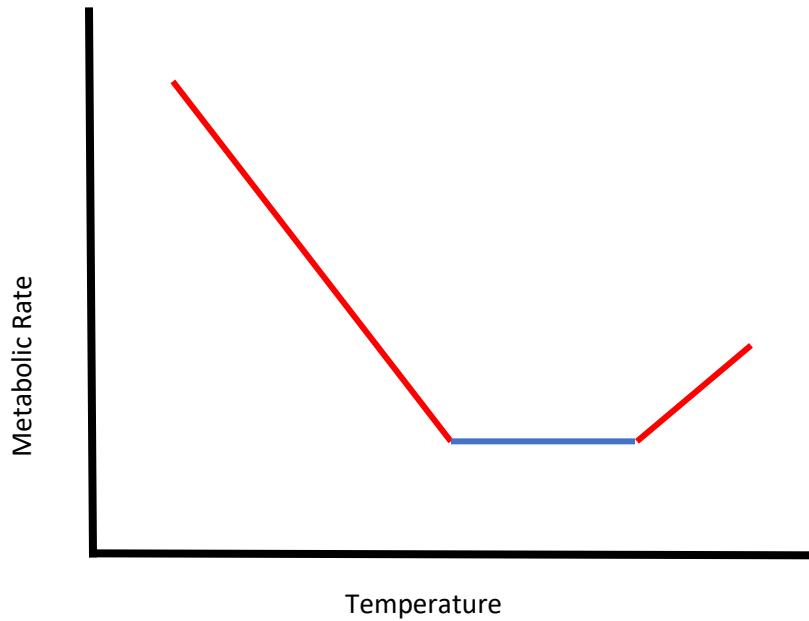


Figure 1.1 A model of resting metabolic rate of an average endotherm at varying ambient temperatures adapted from (Sealander 1951b). The blue portion on the line indicates the thermoneutral zone.

Vasomotion, consisting of vasodilation and vasoconstriction, is the process by which the volume of blood flowing through animals' blood vessels changes. Vasodilation opens the blood vessels so that more blood can flow, whereas vasoconstriction closes the blood vessels so that less blood will be able to flow through (Sealander 1951a). Vasomotion is important in regulating heat loss, especially in highly vascularized appendages, called thermal windows, which can be used to increase heat dissipation (Tattersall et al. 2017). The jack rabbit's (*Lepus arlleni*) ears are prime examples of thermal windows (Dawson and Schmidt-Nielsen 1966). When jackrabbits begin to get warmer, the vessels in their ears vasodilate to allow for greater amounts of heat to dissipate. The opposite is true as well; in cold temperatures, the jackrabbits' vessels vasoconstrict to retain more heat. Temperature control is necessary for animals to maintain homeostasis. Thermoregulatory processes, like vasomotion, help to regulate body temperature. In some cases,

precise thermoregulation is required, and the temperature of animals' appendages can differ from their core body temperature. For example, ungulates hooves can get much colder than the internal body temperature (Cain et al. 2006). One interesting case is when desert or hot-adapted ungulates ideal brain temperature is maintained despite their body temperature becoming hyperthermic (Hetem et al. 2012). Selective brain cooling is accomplished by having a different set of blood vessels going to the brain that are cooled before reaching the head. At high temperatures, above body temperature, heat cannot passively diffuse from the body of an animal to its surroundings; therefore, to release heat at high temperatures, animals use evaporative water loss (EWL) to increase heat loss. The water can be released by sweating, panting, or licking. This water carries energy as heat from the body thereby reducing the temperature of the body and releasing heat in the form of evaporation (Tattersall et al. 2012).

Endotherms also have the capability to huddle. Since endotherms create their own heat, gathering in a small cluster decreases exposed surface area while sharing the energetic costs of producing heat (Eppley et al. 2017). Huddling may even be one reason animals evolved to be social. In the case of the barbary macaques, Campbell et al (2018) showed that the individuals that groomed more and were more interactive with others had bigger huddles and were much more likely to survive the winters (Campbell et al. 2018). Similarly, asocial Abert's squirrels (*Sciurus abertii*) will use communal nesting if ambient temperatures are cold enough (Edelman and Koprowski 2007). As temperature decreased, the Abert's squirrels communal nesting behaviors increased (Edelman and Koprowski 2007).

To understand the relationship between environmental temperature and metabolism, scientists examine how animals gain or dissipate heat. The mechanism by which animals regulate temperature is called a thermal profile. Endotherms have a TNZ (Figure 1.1), which is a range of

ambient temperature that allows for the lowest possible metabolic rate to maintain ideal internal body temperatures. Below the TNZ, endotherms create heat and decrease conductance, effectively increasing metabolic rate and expending excess energy specifically for thermoregulatory purposes (Scholander et al. 1950). The rate at which heat can flow between the air and the animal is described as the animal's thermal conductance; a lower conductance means that less heat can flow between the animal and its surroundings. Above the TNZ, animals increase conductance, via vasodilation and postural changes, to release heat, or increase evaporative heat loss by sweating (Scholander et al. 1950). Sweating can increase the metabolic rate of endotherms. Fat and other forms of insulation can help reduce conductance. Fat provides a thick layer between internal body temperatures and ambient temperatures that decreases heat loss at colder temperatures. The content of the fat also affects the level of insulation it provides and the fat content of mice can shift in different seasons (Hill 1983). The visceral fat is the first fuel burned at low ambient temperature and the fat in the periphery also has a lower melting point than core fat (Sealand 1951b). Using the core fat first allows the mice to increase heat production in a highly vascularized area that can then transport the heat to the rest of the body, and the lower melting point of the peripheral fat allows it to be easily shifted and moved to other bodily locations (Sealand 1951b). To manage heat load without changing their metabolism, the thermal conductance can change in animals to lower or raise the heat loss (Herreid II and Kessel 1967; Bartholomew and Rainy 1971). Changing conductance can involve long term changes, such as winter and summer coats of fur (Lovegrove 2005; Boyles and Bakken 2007). Short term changes involve piloerection or simply changing the body's positioning to expose or cover a larger portion of the body (Tattersall et al. 2012).



Endothermy can be broken further into homeothermic and heterothermic animals. Homeothermic animals have low fluctuation in body temperature whereas heterothermic animals have wide ranges of body temperature (Ruf and Geiser 2015). Torpor is a state of reduced metabolic rate that helps animals save energy in times of poor environmental conditions or poor resource availability (Levesque et al. 2017). A variety of animals use torpor to avoid poor conditions or to save energy daily (Ruf and Geiser 2015).

There are many forms of heterothermy; one form is facultative hyperthermia, regulated increases in body temperature, to decrease the need for evaporative cooling (Bartholomew and Rainy 1971; Chappell and Bartholomew 1980; Gerson et al. 2019). In the case of the antelope ground squirrel (*Ammospermophilus leucurus*), facultative hyperthermia allows for the squirrel to stay active at higher body temperatures to forage for food during the day, after which the squirrel can dissipate large amounts of heat in a cooler underground burrow (Chappell and Bartholomew 1980). Increasing body temperature at high ambient temperature climates increases the gradient between body temperature and ambient temperature, which allows for heat to continue to flow from the body to the surroundings without the need for water (Gerson et al. 2019). Other ways to increase conductive heat loss are by reducing insulative layers, increasing vasodilation, or increasing the amount of exposed surface area (Tattersall et al. 2012).

My thesis aims to create a better understanding of thermoregulation in mice using modern respirometry equipment with thermal imaging to create a wholistic view of the thermoregulatory patterns displayed at high ambient temperature for lab (*Mus musculus*) and field mice (*Peromyscus spp.*). Mice are an ideal study subject because their wide population range and their small size allows for studies in a lab setting. Thermal imaging provides information about the changing thermal windows of the body as animals experience higher

temperatures. Looking at the metabolic data obtained via respirometry, it is possible to see the changes made in energy consumption and relate those changes to the physical changes in body temperature. Understanding how the mice thermoregulate might provide evidence as to thermoregulatory roles of different appendages in the body.

### **Study Species**

*Peromyscus leucopus* and *Peromyscus maniculatus*, the white-footed and deer mouse, respectively, are both small nocturnal mammals. Deer mice are endemic to the northeast of North America but white-footed mice are slowly moving northward into new ranges due to climate-related causes (Roy-Dufresne et al. 2013, Figure 1.2). The white-footed mice and deer mice are potential vectors for the Lyme disease bacteria (Bosler et al. 1984). Studying these two species allows us to understand their range limits and map the potential of Lyme disease transmission into new areas. Gathering data on metabolic rates at varying temperatures would allow us to determine the range of both species.



Figure 1.2: Range map of *Peromyscus maniculatus*. IUCN (International Union for Conservation of Nature) 2009. *Peromyscus maniculatus*. The IUCN Red List of Threatened Species. Version 2019-2.



Figure 1.3: Range map of *Peromyscus leucopus*. IUCN (International Union for Conservation of Nature) 2008. *Peromyscus leucopus*. The IUCN Red List of Threatened Species. Version 2019-2.

As reviewed in Chapter 2 below, much is known about the metabolism, thermal regulation, and behavior of deer mice at colder temperatures but thermal regulation and metabolic rate data at high-end temperatures for both *P. leucopus* and *maniculatus* are scarce. In the literature, there is no information on upper critical limits of the thermoneutral zone for either species. Most of the temperature-related studies on these species are based on activity, performance, optimal foraging, and range expansions (Chappell 2004; Roy-Dufresne et al. 2013; St Juliana and Mitchell 2016).

Using mice as a model species for future thermoregulatory work is ideal because of their size and availability. Due to the mice's size, it is easy to keep them contained in an enclosed respirometry chamber and run thermal imaging at the same time. Working out the methods on a relatively easy species may help create more potential techniques for larger species in the future.

### **Thermal Imaging and Respirometry**

Thermal imaging can be used on animals to monitor skin temperature non-invasively and allows for efficient gathering of temperature data in the field as well as the lab (McCafferty 2007). In the case of ectotherms, skin temperature is often similar to the internal temperature; however, for endotherms, skin temperature does not represent an accurate internal temperature but it may be possible to get internal temperature using the eyes of an endothermic animal (McCafferty 2007). Thermal imaging can also provide insight into thermal windows (McCafferty 2007; Tattersall et al. 2012). For example, thermal imaging has been used to demonstrate that the bill of birds is a thermal window (Tattersall et al. 2009, 2017) as well as the middle digit of the aye-aye's hand (Moritz and Dominy 2012). Thermal windows can potentially explain some thermoregulatory properties that animals can use, like how they handle high ambient heat. If

used in conjunction with respirometry, it is possible to create a thermal profile for species that includes: heat conductance, thermal windows, heat production, and metabolism.

### **Objectives of the Thesis**

The original goal of the thesis was to create a model for thermoregulation in the two *Peromyscus* species in Maine. The model would include metabolic data as well as thermal imaging data to understand how energy is spent thermoregulating at high temperatures and how the animals cope outside of the TNZ. Lab mice (*Mus musculus*), strain ROSA-GFP obtained from the Townsend Lab at UMaine, were later added because of a low trapping success rate in the field.

Using respirometry and thermal imaging over a range of ambient temperatures, I collected thermal profiles for *Peromyscus leucopus*, *Peromyscus maniculatus*, and *Mus musculus*. Using respirometry, I measured metabolic data at varying ambient temperatures while using a thermal camera to record skin temperature data. The skin temperature data was used to model how heat dissipates from the body and how that correlates with changes in metabolism. In Chapter 2, I review the literature on what is known about the physiology of *Peromyscus*. In Chapter 3, I cover the methods for creating a thermal profile of the mice species. In Chapter 4, I present the results of my study and discuss their relevance to the wider field.

## CHAPTER 2

### THERMAL PHYSIOLOGY OF THE *PEROMYSCUS* GENUS

The rodents deer mice (*Peromyscus maniculatus*) and white-footed mice (*Peromyscus leucopus*) are both widely studied because of their great range and diversity of habitats. Studies range from optimal foraging (St Juliana and Mitchell 2016), brown adipose tissue (Van Sant and Hammond 2008), cold acclimation (Sealander 1951b), heat acclimation (Roberts and Chaffee 1976), and ecology (Brower and Cade 2018), to name a few. In this chapter, I review the literature based around thermoregulation in *Peromyscus*.

*Peromyscus* can be found in every major ecosystem in North America, from mountains to meadows to forests, meaning that the deer mice and white-footed mice cover a wide range of climatic variables (Hill 1983), making them great study subjects for research into acclimatization to different environments. Having a species that covers such a wide range of climates demonstrates how animals can acclimate to both freezing and hot temperatures. Comparing the thermoregulatory behaviors and physiology within a diverse genus like *Peromyscus* provides information about how much genetics play into thermoregulation as well as phenotypic plasticity in animals.

In addition to being major components of the small mammal communities over much of North America, *Peromyscus* are major reservoirs for Lyme disease (Roy-Dufresne et al. 2013). Because Lyme disease is a major health concern to the general public, understanding ticks and the white footed mice's range will allow us to inform the public about the potential spread of Lyme disease. Knowing the range distribution for white-footed mice can help us better prepare the public for understanding how to protect themselves from Lyme as well as where Lyme is likely to be found. To create a projected range map of where *Peromyscus* can potentially live, we

need to understand the mice's physiology, their tolerance for climatic variables, and how these affect their current distribution patterns. With current warming climates, white-footed mice have been able to move further poleward potentially exposing new areas to Lyme disease (Roy-Dufresne et al. 2013).

*Peromyscus leucopus* and *maniculatus* currently have a large range (Figure 1.2) in which they are exposed to a variety of temperatures to which they acclimate. *Peromyscus* that are acclimated to the cold have high metabolic rates compared to warm-acclimated mice (Sealander 1951b), as being in the cold requires more metabolic output to keep a warm enough body temperature. Acclimation to heat decreases metabolic rate and may lead to thinner fur (Roberts and Chaffee 1976); reducing the metabolic rate in warm climates allows the mice to remain cooler. *Peromyscus* also experience differing amounts of variability in their climates. Increased variability within a climate causes animals to be more tolerant of hot and cold climates (McNab and Morrison 1963). Being exposed to a variety of temperatures allows for animals to acclimate to different temperatures.

Bergmann's and Allen's rules describe the physical effects of different climates (Rezende and Bacigalupe 2015). In the case of *Mus musculus*, tail length has been shown to decrease in colder climates (Serrat 2013). Colder climates lead to reduced appendage length and an overall decrease in surface area to volume ratio of the body. The decrease in appendage length decreases the area from which heat can dissipate effectively saving energy by not wasting heat. The decrease in surface area to volume ratio has the same effect by decreasing how much heat can be lost to the surroundings. Decreasing surface area to volume ratio can be accomplished by reducing the exposed surface area of any part of the body; this is commonly achieved by curling into a ball. McNab and Morrison (1963) added the observation that a curled-up *Peromyscus* can

reduce its exposed surface area by up to 7/10. Internal bodily changes included, decreasing organ size is mostly seen in the heart, liver, and the kidney (Roberts and Chaffee 1976). Furthermore, behavioral thermoregulation is more efficient than physiological thermoregulation. Behavioral thermoregulation does not require any loss of water and barely uses any energy. Behaviors include using microclimates, activity, huddling, and postural changes, to name a few (Tattersall et al. 2012). White-footed mice are known to huddle as newborns, which helps them mature and develop properly (Hill 1983). When provided with a choice, *Peromyscus* prefer temperatures within their TNZ (St Juliana and Mitchell 2016). However, this preferred temperature can change through time because of a variety of factors, like lack of food (Hamilton and Sheriff 1959) or changes to the thyroid (Laties and Weiss 1959).

Temperature is not the only stimulus that animals respond to by using thermoregulatory changes. When exposed to novel environments, the body temperature of *Peromyscus maniculatus* increases; the same occurred when exposed to social rivals (Andrews 1978). Even minor changes in the body temperature of the mice results in a large increase in metabolic rate. Mice use shortening day length to stop reproduction (Kaseloo et al. 2014). Certain subspecies of the *Peromyscus* will continue reproduction into the winter months, which leads to consistent increases in their metabolic costs to maintain reproductivity (Kaseloo et al. 2014). Heterothermic animals do not regulate body temperature as closely as a homeotherm; instead, heterotherms allow their body temperature to shift to save energy. *Peromyscus leucopus* and *maniculatus* body temperatures vary depending on the ambient temperature and if they are torpid. Deer mice, however, will not go torpid if there is food ad libitum (Ruf and Geiser 2015). The deer mice only go torpid after losing 10% of their body fat (Emil Morhardt 1970). White-footed mice will go torpid solely based on the stimulus of temperature and are excellent at gaining fat quickly (Emil



Morhardt 1970). However during confinement, there was no apparent circadian effect on the body temperature of the mice (Morrison et al. 1957).

A major physiological thermoregulatory property is insulation, which is provided by adipose tissues and fur. Although the fur content can change through seasons, the change takes too long to be beneficial to any short term or rapid changes in temperature (Sealander 1951b). Altitudinal differences, over about 10,000 foot elevation difference, had negligible effect on pelage between montane *Peromyscus maniculatus* and coastal *Peromyscus maniculatus* (Murie 1961).

Unlike cold temperatures warmer temperatures require more water to remain in homeostasis. To cope with high-end temperatures, *Peromyscus* will increase panting as well as salivation in a laboratory setting (Sealander 1951b). The saliva is used to lick the arms and chest to reduce skin temperature and increase evaporative heat loss. Another strategy to dealing with high ambient temperature is vasodilation, which increases conductive heat loss (Tattersall et al. 2012). Blood flow to the periphery has been shown to increase in mice when in high ambient temperatures (Sealander 1951a, Figure 2.1). Desert species must consistently deal with high-end temperatures from both ambient temperature as well as strong radiation (Murie 1961). In addition to extreme temperature stress, desert species have limited access to water. One way mice and other species have dealt with constant high temperatures is facultative hyperthermia (Murie 1961). Raising body temperature when ambient temperature is hotter than body temperature allows for a smaller temperature difference, which reduces the conductance of the animals.

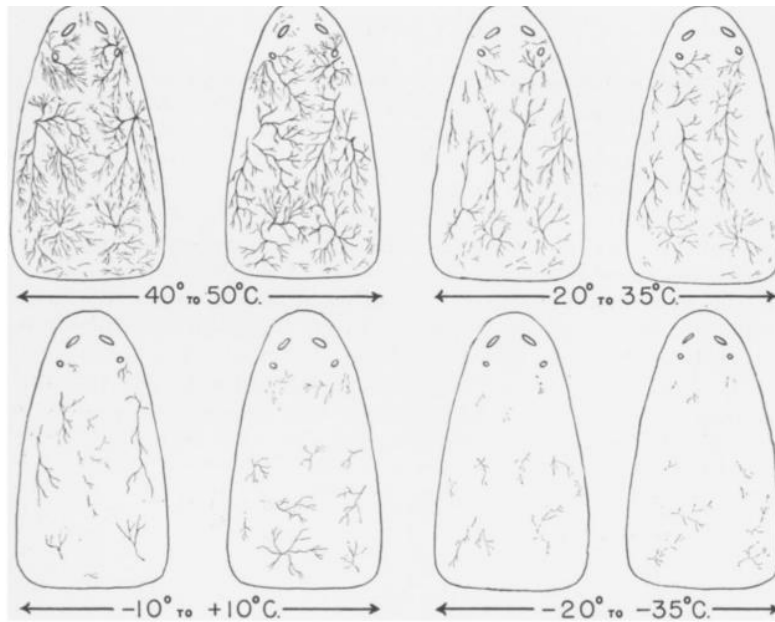


Fig. 6.—Appearance of the cutaneous blood vessels in *P. l. noveboracensis* after death without food or water at different air temperatures.

Figure 2.1: Picture of blood vessels at varying temperatures from (Sealander 1951a).

Considering that juvenile mice have a very low survival rate, it is hard to gather data on thermoregulation in young mice (Hill 1983). Young mice are precocial and require parental care for the first two weeks of their life; during this time, the mother and the young huddle in nests (Hill 1983). If the young are exposed to low ambient temperatures, they have stunted growth as well as a stunted thermogenic capacity (Hill 1983).

The *Peromyscus leucopus* and *maniculatus* have well-documented thermal physiology; however, most of the information I was able to find was from the mid-1900's and focused on colder temperatures. Because of how the climate is changing, examination of hotter temperatures is warranted. In the next chapter, I attempt to measure the thermal profile of *Peromyscus maniculatus* and *leucopus* in Maine, using modern flow through respirometry in conjunction with thermal imaging to examine heat loss in the context of changing metabolic outputs.

## CHAPTER 3

### THERMAL IMAGING AND RESPIROMETRY METHODS

Sherman live traps (H.B. Sherman Traps, Inc.; Tallahassee, FL) were baited with peanut butter and oats and filled with five cotton balls to provide insulation. Traps were set in the Dwight B. Demeritt Forest and University of Maine Experimental Forest for 8-10 hours (about 19:00 to 05:00). Bycatch animals included flying squirrels, voles, shrews, and moles, which were released immediately at the site they were trapped. Measurements included: forearm, foot, heel to toe-pad length; ear length; distance between the urogenital opening and the anus (an indication of sex); and mass. Reproductive status in females was determined by the presence of nipples and above average weight. Reproductive females were released after measurements. Males and non-reproductive females were injected with a passive integrated transponder (PIT) tag (BioThermo13, Biomark; Boise, ID) in the scapular region and brought back to the lab. PIT tags were used to gather subcutaneous body temperatures with a Biomark (Biomark, Inc.; Boise, ID) PIT tag reader. In the lab, they were weighed again for accuracy. Mice were kept in a plastic container with a slice of apple for one hour then fasted for two hours before beginning respirometry. *Peromyscus maniculatus* and *leucopus* were indistinguishable based solely on morphometrics. Ear punches (3 mm) were collected for the purpose of genetic testing but, due to time constraints, the tests were not yet run. Lab mice were fitted with a PIT tag and fasted for an hour before being placed in the respirometry chamber.

#### Respirometry

Fasted animals were placed in an airtight respirometry chamber (1.2 L) on a grate above mineral oil. The mineral oil reduces the change in water pressure caused by excrement. The chamber consisted of a plastic container with tubing connectors and sealed using plastic wrap so that the

lid was permeable to infra-red. The mouse chamber had in-flow from a pump with the flow controlled by an Alicat (MC-Gas Mass Flow Controllers, Alicat Scientific; Tucson, AZ), flow rate at 1260 mL/min, from outside air for all temperatures. The outside air was filtered through Drierite™ ( $\geq 98\%$  CaSO<sub>4</sub>,  $< 2\%$  CoCl<sub>2</sub>; W.A. Hammond Drierite Co., Ltd.; Xenia, OH) to remove all water content. The air from the mouse chamber then flowed to the sub-sampler (SS-4 Subampler, Sable Systems; North Las Vegas, NV), which shifted the flow between a control airstream and the mouse chamber at 5 min and 40 min intervals, respectively. After the subsampler, the air flowed into a gas analyzer (LI-840A CO<sub>2</sub>/H<sub>2</sub>O Gas Analyzer, LI-COR; Lincoln, NE), which records water content and carbon dioxide. Then, after going through more drierite, oxygen was analyzed with the oxygen analyzer (FC-10 Oxygen Analyzer, Sable Systems; North Las Vegas, NV).

The airtight container was placed in a large cooler box that was equipped with a Pelt 5 (Sable Systems; North Las Vegas, NV) heating unit to control the temperature of the cooler box. Temperatures tested were 25, 30, and 35°C; the Pelt5 was set to 0.5°C higher than desired to get the temperature of the mouse container up to the experimental temperatures. The mice were tested at each temperature for 50 minutes each, consisting of a 5-minute baseline at the beginning and end of the experiment and a 40-minute data collection period. The Licor's CO<sub>2</sub> analyzer was calibrated using pure oxygen and then a high CO<sub>2</sub> span gas (19000 ppm). The Licor's water readings were calibrated using pure oxygen as a zero and water vapor of known dew point for as a span.

### **Thermal Imaging**

Using a FLIR T62101 camera (FLIR systems. Inc.; Wilsonville, OR), a thermal video was taken of the mice during the respirometry trials. The video was taken during the 40 minutes of data

collection at each temperature: 25, 30, and 35°C. The camera was placed 40 cm above the mouse. The video was analyzed using the ResearchIR program provided by FLIR. The data were analyzed at the resting state determined by the respirometry, or the lowest oxygen consumption for 10 minutes. During the resting state, six images were analyzed, taken about two minutes apart from each other. The six images were chosen based on the positioning of the mouse, ideally trying to get as much of the mouse to be visible as possible. The surface temperature was gathered for the back of the mouse, the foot, and the tail, as well as the surrounding temperature.

### **Data analysis**

VO<sub>2</sub> was calculated using the equation (Lighton 2008):

$$VO_2 = FR_i \left( F_i O_2 - \left( \frac{F_e O_2 (1 - F_i O_2 - F_i CO_2 - F_i H_2O)}{(1 - F_e O_2 - F_e CO_2 - F_e H_2O)} \right) \right)$$

where FR<sub>i</sub> is the in-flow, F<sub>i</sub> is the proportion of O<sub>2</sub>, CO<sub>2</sub>, or H<sub>2</sub>O in the in-flow, and F<sub>e</sub> is the excurrent proportion. The data were taken from a 10-minute portion of time that had the lowest metabolic rate as determined using the “2-point baselining function” in Expedata Data Analysis Software (Sable Systems) and a custom macro that selected the 10 lowest continuous measurements from each temperature. The 10-minute low was then averaged to get a single point.

Thermal images were analyzed using the ResearchIR program provided by FLIR. The images were analyzed in sections, based on the back, the leg, and the tail. The data gathered from the program were the mean temperature of each area along with the standard deviation. The heat loss due to radiation was calculated using the following equation (Cross et al. 2016):

$$R = \frac{1}{A} \int E \delta (T_{surf}^4 - T_{surr}^4) dA$$

where  $R$  is heat flux,  $A$  is surface area of the object,  $E$  is emissivity,  $\delta$  is the Boltzmann constant,  $T_{\text{surf}}$  is the temperature of the surface of the animal, and  $T_{\text{surr}}$  is the ambient temperature. All statistical tests and calculations were run in R studio packages “ggplot2” and “segmented” (version 3.5.2; Wickham 2016; Vito 2008).

## CHAPTER 4

### MICE METABOLISM

#### Results

Between May 1<sup>st</sup> and August 1<sup>st</sup>, 2019, a total of five *Peromyscus* (which could not be identified to species) were caught: three males and two lactating females, the latter which were not included in the study. Mass of the mice (15.1-18 g) was included in all calculations. Heat flux (W) for the mice was calculated from the three *Peromyscus* and found to be much larger in the back when compared to the tail and feet. However, the feet and tail had a greater heat loss per unit area. At 35°C, subcutaneous temperature, measured via the PIT tags varied from 36-37°C and eye temperature from 37-38°C.

#### VO<sub>2</sub>

Field mice had the lowest metabolic rates at 30°C and the highest at 35°C. The metabolic rate of lab mice did not change across the temperatures. At 35°C, field mice had the highest VO<sub>2</sub> whereas lab mice had a consistent VO<sub>2</sub> (Table 3.1). All mice showed either an increase in VO<sub>2</sub> or a steady VO<sub>2</sub> from 30°C to 35°C (Figure 3.1).

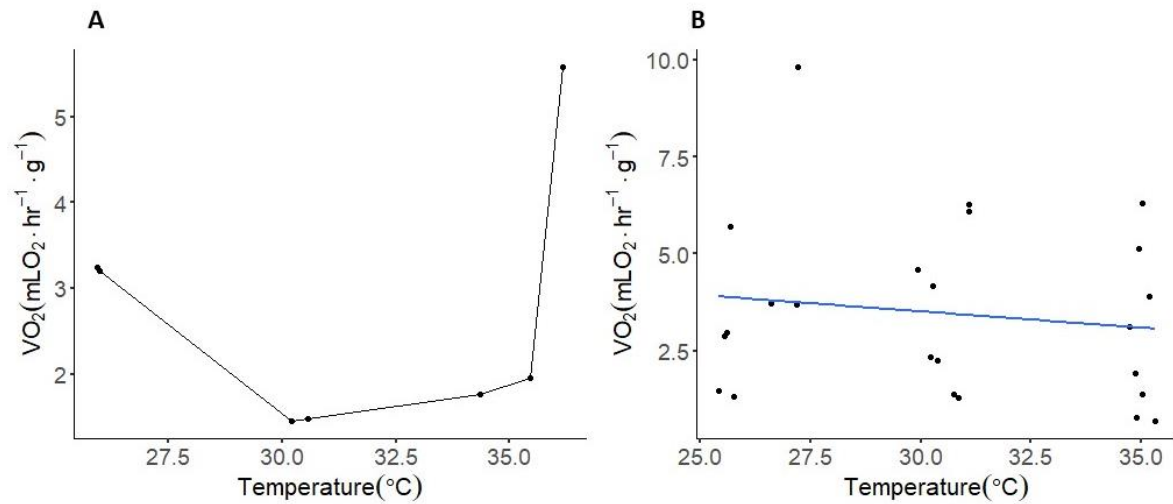


Figure 3.1: Resting metabolic rates of two small rodents at varying temperatures. The VO<sub>2</sub> was calculated in a fasted and resting state. (A) represents field mice specimens (n=3) and (B) represents the lab mice (n=8). Each point is a 10-minute window at each temperature for a mouse; therefore, each mouse has three points, one at each temperature (25, 30, and 35°C)

Table3.1: Respirometry data from field mice and lab mice. Respirometry was run on three field mice (*Peromyscus spp.*) and eight lab mice (*Mus musculus*). Mice were rested and fasted during the respirometry. All values were averaged, with the standard deviation, amongst the field mice or the lab mice.

Type	Temp (°C)	VO <sub>2</sub> (mL*hr <sup>-1</sup> * g <sup>-1</sup> )	EWL (mLH <sub>2</sub> O*hr <sup>-1</sup> *g <sup>-1</sup> )	Mean Mass (g)
Field	25	56.37±9.23	0.00167±0.0004	16.9±1.57
Field	30	25.97±3.37	0.00119±0.0002	16.9±1.57
Field	35	53.44±32.091	0.00269±0.0009	16.9±1.57
Lab	25	69.587±26.66	0.0047±0.0023	22.79±2.77
Lab	30	69.58±36.66	0.0047±0.0002	22.79±2.77
Lab	35	62.42±36.75	0.0044±0.0003	22.79±2.77

## EWL

The evaporative water loss of the field mice had a positive correlation with temperature. Lab mice showed no correlation between EWL and temperature. All mice showed an increase in EWL from 30°C to 35°C with the lab mice showing a less substantial increase (Figure 3.2).



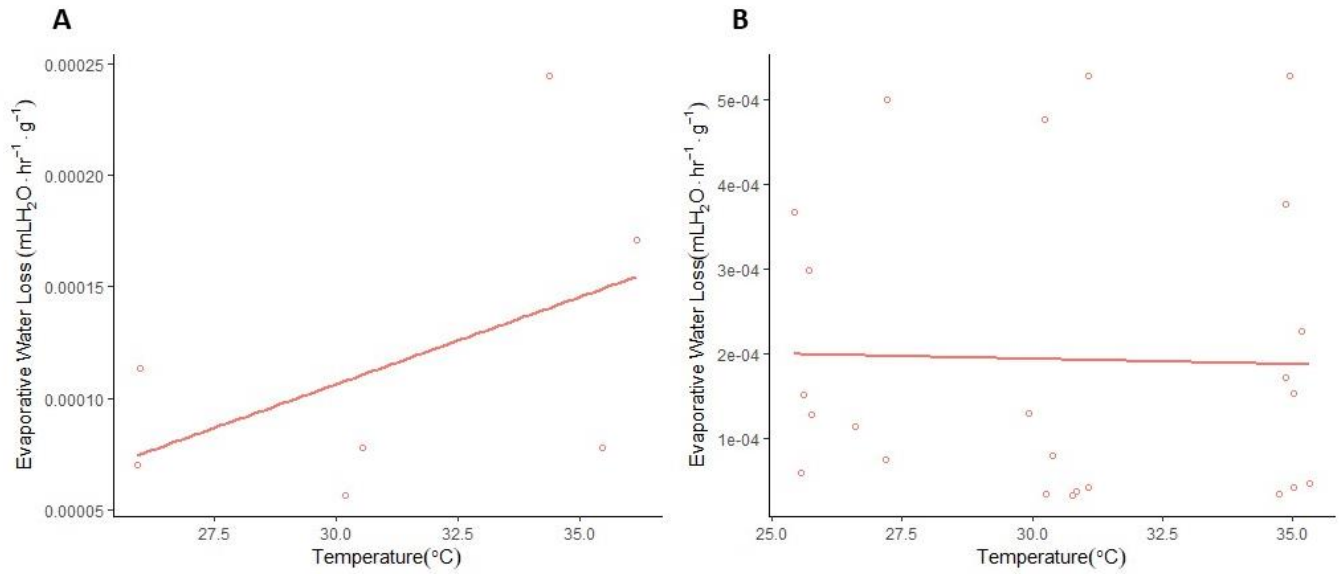


Figure 3.2: Evaporative water loss at varying temperatures (°C) for eight *Mus musculus* and three *Peromyscus* spp. A: data from field mice and B: data from lab mice. Each point on the graph is a 10-minute average of one mouse at each temperature. Lines represent a general trend.

### Radiative Heat Loss

More heat was lost through the back of the *Peromyscus* compared to the tail (Figure 3.3). The back had the greatest difference in temperature when compared with the temperature of the chamber. The back had an average temperature difference of  $3.14 \pm 1.75$  °C while the tail had an average temperature difference of  $2.02 \pm 1.28$  °C.

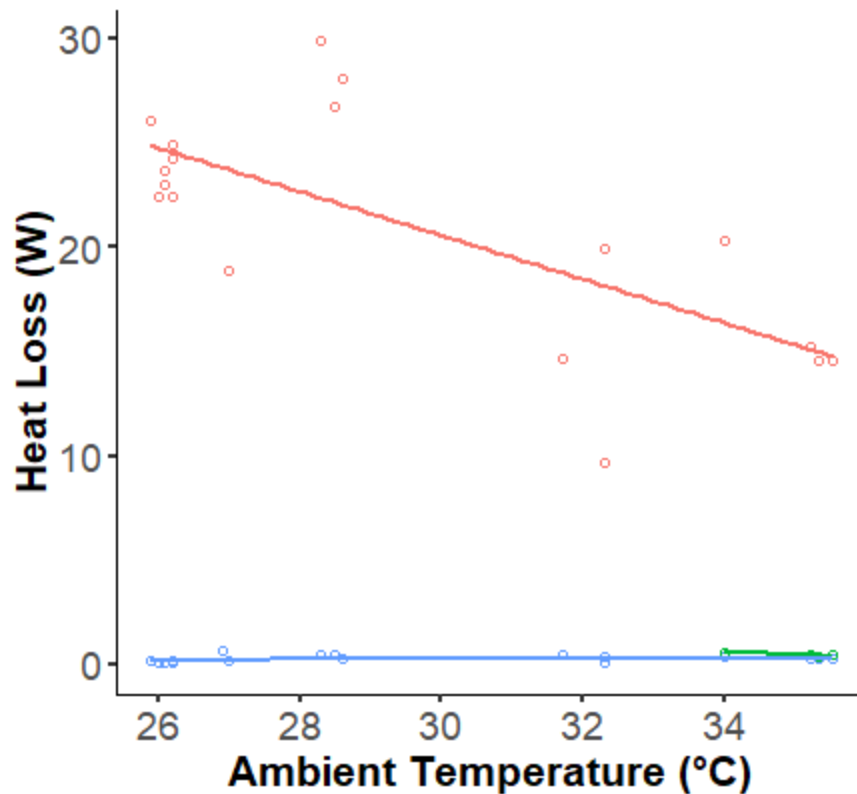


Figure 3.3: Radiative heat loss from the back (red), tail (blue), and foot (green) of a single field mouse over a range of ambient temperatures (n=3). Each point on the graph is a specific image, each mouse had six images for each of the three temperatures for a total of 18 images per area on the mouse, besides the foot which was only available at high temperatures.

With a sample size of three *Peromyscus* and eight *Mus musculus*, it was found that there was a general trend for lab mice to have higher rates of evaporative water loss ( $p=0.0935$ ) and larger  $VO_2$  ( $p=0.2964$ ) compared with the field mice.

## Discussion

Due to the high levels of activity observed at the 25°C for all mice, the  $VO_2$  appeared much larger than what was described in the literature. Activity was not recorded however, it was monitored through simple observations of activity over time. All mice placed in the chamber were active for the first 10 minutes. Therefore, the high rate of metabolism at this temperature

may be the result of activity. Field mice had the lowest metabolic rate at 30°C, with increases at both the highest and lowest temperatures measured. The back of the mouse created the greatest amount of heat flux from the body due mostly to its greater surface area when compared with the tail and feet. Water loss showed a positive correlation with temperature for field mice. Lab mice had little to no correlation between metabolic rate and temperature nor evaporative water loss and temperature at the temperatures measured.

Previous work indicated that *Peromyscus* have a TNZ of about 30-34°C (Murie 1961). In the current study, resting metabolic rate was lowest at 30°C (Figure 3.1). Since the lowest metabolic rate was at 30°C, these data corroborate the TNZ found by Murie (1961) who also recorded dip in metabolism in that range. It is possible that 25°C would have produced a metabolic rate similar to 30°C but the mice were not given enough time to settle in to the respirometry chamber. At the beginning of the experiment, the mice were active and, if given more time, may have become accustomed to the surroundings before respirometry started. All of the field mice showed a clear metabolic increase at 35°C (Figure 3.1). Additionally, at 35°C, all the mice stretched out, exposing the majority of their body to dissipate heat more effectively. Even though this postural change likely helped dissipate more heat, because the ambient temperature is closer to body temperature at 35°C, heat flux from the back was lower compared with 30°C. Field mice had lower metabolic rates at all temperatures when compared with lab mice. Lab mice are fed ad libitum, meaning that the lab mice can afford to have a high metabolism and still eat enough to meet those needs. However, field mice cannot eat whenever and likely go long periods of time without food (St Juliana and Mitchell 2016). If the field mice had higher metabolic demands, it is possible the field mice would not be able to eat enough to keep up with the increased metabolic costs.

The lab mice had higher water loss rates than the field mice (Table 3.1). Evaporative water loss helps reduce body temperature at the cost of water (Cain et al. 2006; Mitchell et al. 2018). Lab mice that are fed ad libitum have a constant supply of water and do experience high ambient temperatures whereas field mice are exposed to high ambient temperatures during the summer months with the potential for lack of water. Since the lab mice had no correlation between metabolism and temperature and no correlation between water loss and temperature, it is possible that the temperatures tested reside within, or close to, the TNZ for the species. If these temperatures were within the TNZ, then the TNZ for these species is much larger than reported in previous studies (Gordon 2012).

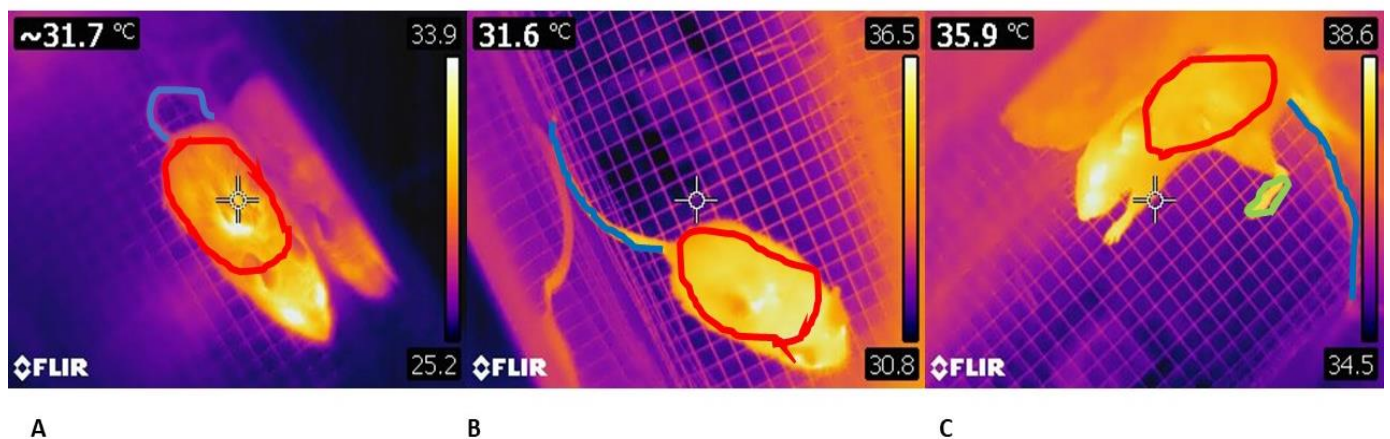


Figure 3.4: *Peromyscus* at 25°C (A), 30°C (B), and 35°C (C). The temperature gradient legend is different for each image. The number in the top left of each picture indicates the temperature at the center of the picture. The polygons drawn onto the images are the areas that were used for heat loss calculations. Red represents the back, blue the tail, and green the foot.

The mice were able to dissipate more heat from the backs than the extremities. Not only does the back cover a much larger area over which heat can be dissipated, it was also consistently warmer than the extremities (Figure 3.4). The difference in temperature between the body and its surroundings determines the rate and direction of heat transfer. If the body temperature is much higher than the surroundings, the heat loss will be much greater than if the

body temperature is equal to the surrounding temperatures. Since the back was warmer than the extremities, the back was also releasing more heat per unit area. Blood vessels in *P. leucopus* can dilate at high temperatures to allow for more heat dissipation (Figure 2.1). The large vascular bed presented in the images shows how the mice are able to dissipate heat effectively through their back. However, since 35°C is only about 1°C above the TNZ for *leucopus*, it is likely that this experiment did not cover temperatures high enough to show the tail and feet dissipating more heat (Sealander 1951a). It is possible that, at 35°C, the back is more than enough to stabilize body temperature without increasing blood flow to the tail and legs. The mice's tails began to warm up at the base and slowly get hotter towards the tip as the experiment proceeded; this slow progression of blood vessels dilating may demonstrate that the tail is used as a thermal window solely at higher temperatures (Fig3.4A and C). Having extremities dissipate heat during extreme ambient temperatures would allow the core body to remain cooler.

Mice can change their conductance by piloerection, vasodilation, and exposing more of surface area of their body to the environment (Hill 1983; Tattersall et al. 2012). As temperatures increased, the mice would always take a prone position as well as piloerect, which increases the air flow to the skin. An area on the body where heat can be dissipated is considered a thermal window (Tattersall et al. 2017). The original goal of this paper was to examine the idea that the tail plays a large role as a thermal window in mice. Since the tail is hairless and non-prehensile, I believe it may have a role in thermoregulation. The data collected here do not provide enough evidence to support the tail being a primary thermal window even though the tail did begin to increase in temperature the longer the mouse stayed in the chamber at 35°C.

## Conclusions

Metabolic and thermal imaging data can provide extensive amounts of information about thermoregulation within animals. The thermoregulatory information gathered can be used to determine which species may become vulnerable to climate change as well as predict potential range shifts in populations experiencing changing climates (Levesque et al. 2016). With similar data collected over a wider range of ambient temperatures, I could find the upper critical limit of the mice, which would provide insight into potential northern expansions of the populations. The back of the mice had the highest heat flux of any body part. Tail temperature increased the longer the mouse stayed at 35°C, indicating that the tail may be used as a secondary thermal window. Thermal imaging should become widely used to allow for non-invasive thermoregulatory studies. While lab mice are good study subjects due to convenience and availability, they are not like wild species. Because of these differences data gathered from lab mice cannot be extrapolated to predict changes in field mice. Lab mice had higher metabolic rates as well as higher evaporative water loss than field mice.

Future studies should aim to use thermal imaging and respirometry to create more complete thermal profiles for any vulnerable species. Thermal imaging technology is beginning to open new tests for the field of metabolism/thermoregulation. Thermal imaging is a non-invasive way to collect temperature data from long distances making it ideal for field use on larger animals. Understanding the physiological limitations of a species thermoregulatory control can identify vulnerable species in the face of increasing global temperatures. Studies can also focus on more applications of thermal imaging. Now that thermal imaging is more accessible for scientific studies, it may be used to gather body temperature data in the wild for any animal. Thermal imaging may even be able to detect health problems, like tumors, or examine different

thermoregulatory patterns between individuals (McCafferty 2007). Thermal imaging and respirometry technologies are constantly advancing and should be used to create holistic thermal profiles to understand how animals will experience the upcoming climatic changes.

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Jake Gutkes was raised in the New York City, New Jersey area. Graduating Toms River High School North in 2015 he went on to get his Bachelors of Science in Zoology from the University of Maine in 2018. He began his work with Dr. Danielle Levesque in 2017, during his undergrad, working with thermal imaging in tenrecs, then continued his research into thermal imaging of mice the following year for his Master's research. After receiving his degree Jake plans on searching for PhD positions in the field of primatology focusing on behavioral and social changes based on temperature. Jake is a candidate for the Master's of science in Zoology from the University of Maine in December of 2019.